Some procedural Problems in the Study of Tetrapod Origins

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The historical method of phylogenetic analysis is discussed. It is illustrated by palaeontological, embryological, comparative anatomical, and morphofunctional investigations of rhipidistians and amphibians. Rhipidistians and amphibians (both urodeles and anurans) have some common morphogenetic features that suggest a close phylogenetic relationship.

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For several years now, the methods of 'phylogenetic systematics' have been applied extensively to the study of early vertebrates, often with results different from those produced by 'evolutionary' systematists. Nowhere has this been more marked than in the works of Rosen *et al.* (1981) who attempted to reestablish a closer link between tetrapods and dipnoans than between tetrapods and rhipidistians. In their proposed phylogeny, the Tetrapoda and Dipnoi are regarded as sister groups and together form the Choanata.

These sweeping changes have not had support from many specialists. For instance, Schultze (1981) showed that several of the features on which the argument was based would not carry the weight placed upon them. In particular he questioned the homology of the openings referred to as choanae in the two groups. However, the very fact that such a scheme could be proposed points to the incompleteness of our knowledge of the evolution of early tetrapods and the absence of reliable criteria for phylogenetic reconstruction.

The establishment of homologies must logically precede the discussion of phylogeny (Remane, 1964), but the twin difficulties of avoiding circularity in our arguments and distinguishing between homologous and homoplasious structures (Simpson, 1961; Bock, 1973; Vorob'eva, 1980a) continue to bedevil work in real situations. The phylogenetic weight to be attached to various features remains a problem, especially as structural, functional and ontogenetic aspects of such features all have to be considered. In resolving such problems, the essential first step after deciding on homologues is to establish polarized morphoclines (Hecht and Edwards, 1977) and then to trace lines of evolutionary development.

This programme implies extensive morpho-functional and morpho-ecological study of recent groups. Granted the importance of such studies, it is difficult to accept the cladistic conceptions of Patterson (1977) that all problems of phylogeny should be solved exclusively by study of recent groups, and that palaeontological material cannot be used to falsify these solutions. Palaeontology provides historical documents for the study of evolution and thus exerts a control on neontological speculation as well as providing unique data for phylogenetic reconstruction. These leading roles for palaeontology have been repeatedly demonstrated in the works of the founders of vertebrate evolutionary morphology and palaeontology in the USSR (see Schmalhausen, 1964). The 'historical method' continues to be applied by the whole of the
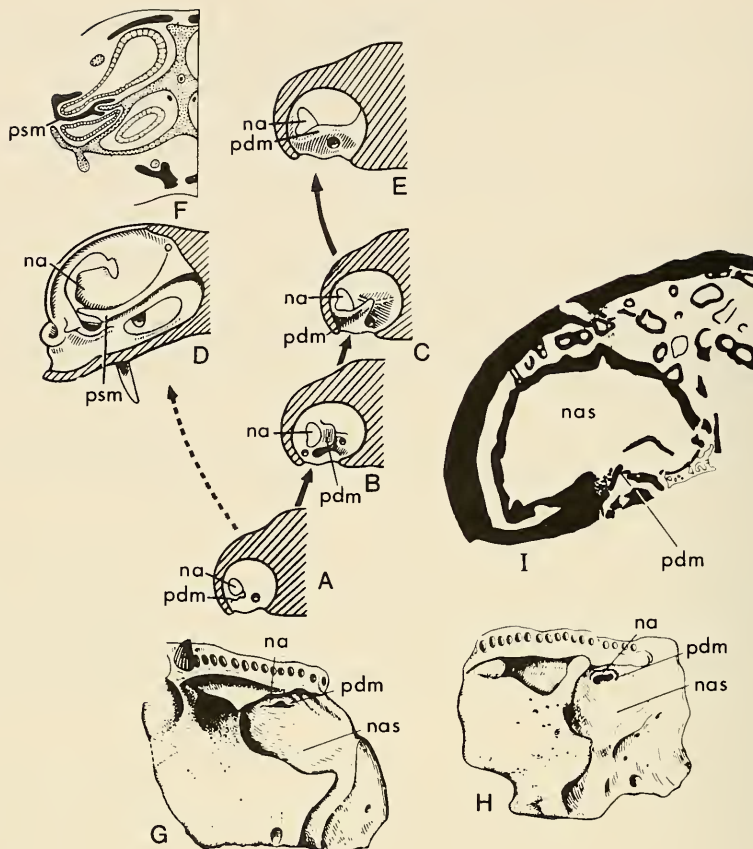
Fig. 1. The different state of the dermintermedial process (pdm) in rhipidistians and the septomaxillar process (psm) in amphibians. Rhipidistians are **A**, *Thursius;* **B**, *Eusthenopteron obruchevi;* **C**, *E. foordi;* **E**, *Platycephalichthys bischoffi;* **G**, *Gyroptychius elgae;* **H**, *Porolepis polonica;* and **I**, *Youngolepis praecursor.* Amphibians are **D**, *Rana,* and **F**, *Hypopachus cuneus. na,* narina anterior; *nas,* nasal capsule (**A,B,E,G**, from Vorob'eva, 1977; **C,D**, from Jarvik, 1942; **H**, from Kulczycki, 1960; **F**, from Jurgens, 1971; **I**, from Chang Mee-Mann, 1982).

Soviet palaeontological and morphological school, as is exemplified by the work of Obruchëv and Schmalhausen and their students.

Fish-tetrapod relationships are at present under examination in the USSR, particularly through study of the historical morphogenesis of the skeleton-muscle systems and receptor organs. Such a study focuses attention on the theoretical problem of the significance of morphogenetic processes for phylogenetic study in general, as well as the functional and ecological meaning of these processes and their significance for the understanding of evolutionary mechanisms. Contributions are being made from the comparative anatomy, comparative and experimental embryology, physiology and morphoecology of fishes, amphibians and reptiles, as well as palaeontological study of crossopterygians and fossil lower tetrapods.

As a result of these studies, several new proposals have emerged. The narrow specialization of some crossopterygians to an amphibian environment may possibly be an 'aromorphic' (Severtsov, 1939) step to a terrestrial way of life (Vorob'eva, 1971,
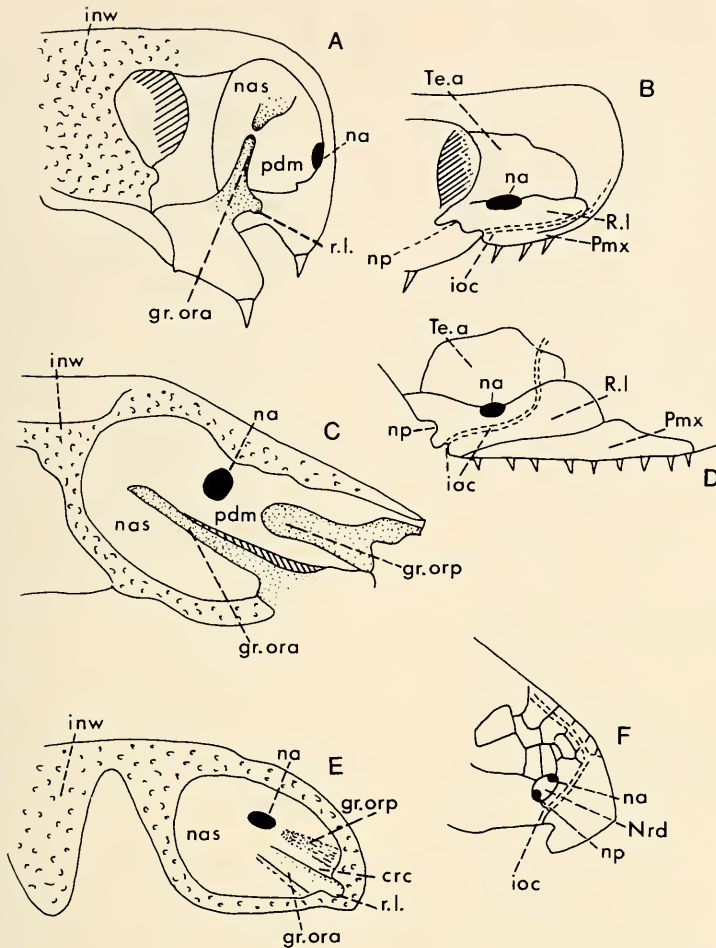
Fig. 2. Similarity and differentiation of the nasal capsule in some rhipidistians. **A,B,** *Panderichthys stolbovi* (from Vorob'eva, 1973), **C,D,** *Powichthys* sp. (from Vorob'eva and Schultze, 1984; **E,F,** *Holoptychius* (from Jarvik, 1980). *gr. ora, gr. orp,* oro-rostral anterior and posterior grooves; *inw,* internasal wall; *ioc,* infraorbital canal; *na, np,* narina anterior, posterior; *nas,* nasal capsule; *Nrd,* nariodal; *pdm,* dermintermedial process; *Pmx,* premaxillary; *R.l.* lateral rostra; *r.l.* lateral recess; *Te.a,* anterior tectal.

1977). The parallelism that often occurs between osteolepid crossopterygians and lower tetrapods may be explained by canalization of morphogenetic mechanisms, and this may be interpreted as an argument favouring the taxonomic propinquity of these groups (Vorob'eva, 1980b). The 'forestall' principle (see below) resulted from the study of crossopterygian material (Vorob'eva, 1980a). The idea of an evolutionary succession of correlated systems in the skulls of crossopterygians, amphibians and reptiles, has been worked out by Lebedkina (1979). The use of functional arguments to identify the homologies of jaw muscles, and the principle of paraconvergent morphological resemblance, have been elaborated (Iordansky, 1982). Smirnov (1984) has proposed extensive heterochrony in the formation of the amphibian middle ear, and the consequences of this idea for the study of changes in crossopterygian skulls have been analysed (Vorob'eva and Smirnov, 1982). Examples of these points follow.

The 'forestall' principle refers to the development of a structure in a taxon more primitive than the one in which it has its characteristic development. It is illustrated by similarity of the dermintermedial process in rhipidistians and the septomaxillary process in anuran and urodele amphibians. A poorly-developed dermintermedial process is found in some Middle Devonian osteolepids (*Gyroptychius pauli, G. elgae, Thursius estonicus* (Vorob'eva, 1977)), and it is also found in some Early Devonian Porolepididae (*Porolepis polonica* Kulczycki, 1960) as well as in *Youngolepis praecursor* (Chang Mee Mann, 1982), which are illustrated in Fig. 1. In the evolution of different lines of osteolepiforms this process becomes stronger until in *Eusthenopteron foordi* it reaches the stage of the septomaxillary process in Anura (*Rana* in particular). In *Platycephalichthys bischoffi* the dermintermedial process fuses with the medial wall of the nasal capsule which is similar to the situation in the microchylid anuran *Hypopachus* (Fig. 1; Jurgens, 1971). In these instances the same degree of structural development is reached independently. Similar examples indicate that this phenomenon is widespread, and results in the well-known mosaic pattern of evolution.

It is important to note that in most osteolepiforms the dermintermedial process develops similarly to the homologous septomaxillary process in Anura, but the majority of porolepiforms differ in that they develop their process in the lateral nasal capsule wall. Jarvik (1980) described a rostro-caudal endocranial crest lying along the lateral wall of the nasal capsule in *Porolepis brevis* and in *Holoptychius*, and this is comparable with the structure in urodeles. Vorob'eva (1973) described a dermintermedial process resembling the above crest in *Panderichthys stolbovi* (Fig. 2), and Vorob'eva and Schultze have been able to show that *Powichthys* has, along the lower edge of the anterior nostril, a well-developed, flat, dermintermedial process which continues caudally into a similar rostro-caudal crest (Fig. 2). This process in *Powichthys* resembles that of *Panderichthys* and probably originated from the lateral rostral, which is present in *Powichthys* but has been lost in porolepids. A dermintermedial process was recorded by Schmalhausen (1958) in the urodele *Onychodactylus fisheri* and by Medvedeva in *Ambystoma*.

A linear sequence in the structural evolution of crossopterygians and tetrapods is also noted by the correlation between the developing exoskeletal and endoskeletal systems in the two groups. A good example is in the morphogenetic similarities of the palatal bones. Jarvik (1954) presented a hypothetical reconstruction of gnathostome palatal and jaw arches (Fig. 3). The arches are isolated and both carry isolated shagreened plates. He assumed that the ancestors of the Rhipidistia showed a similar condition.

Lebedkina (1979: figs 76a, 80) showed that in the larvae of the primitive urodeles *Ranodon* and *Hynobius*, the jaw arch bones (premaxilla), palatal arch (vomer) and parasphenoid, are not linked together. Their force lines which reflect the orientation of collagen fibres and the direction of static forces, do not form an integrated system (Fig. 3**C**). In the upper jaw (premaxilla) and palate (vomer and pterygopalatine) they are oriented parallel with the jaw margins, but in the anterior part of the parasphenoid they are longitudinal. At metamorphosis the vomers are formed with their force lines parallel with those of the parasphenoid. These new vomers lie close to the recently formed process of the premaxillary and later with the parasphenoid (Fig. 3**D**). As a result a new system is formed in which forces are differently transmitted from the jaw arch to the parasphenoid.

In larval dipnoans the force lines of the palatal arch and the parasphenoid are independent (Fig. 3**E**) though the pterygoid lies quite close to the parasphenoid. Lebedkina (1979) thought this primitive condition to be an argument in favour of phylogenetic affinity of dipnoan and crossopterygian ancestors. It has been assumed
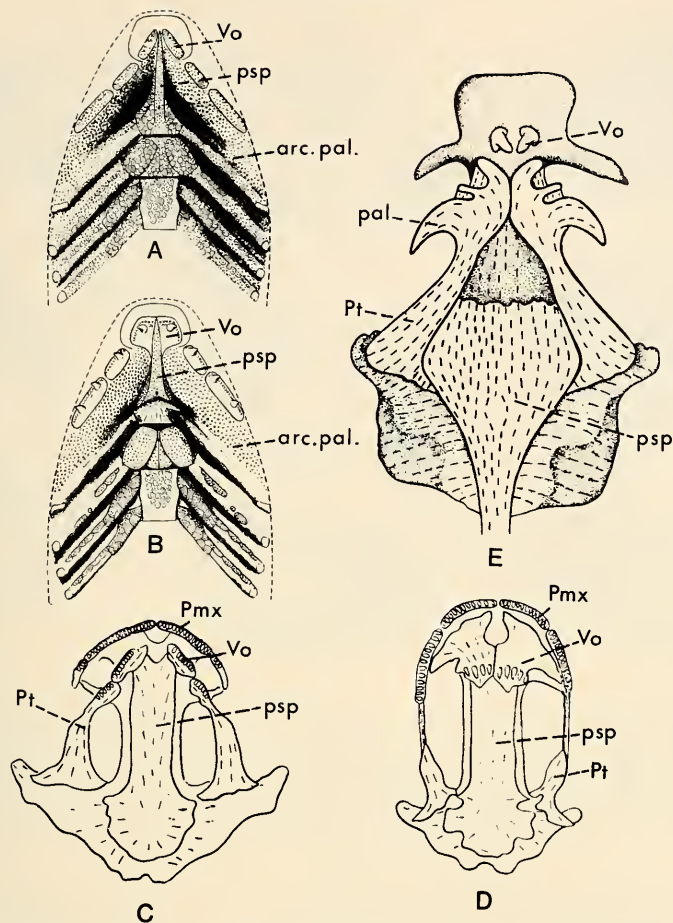
Fig. 3. State and development of the palatal surface in Gnathostomata: **A,** hypothetical primitive condition; **B,** generalized rhipidistian condition; **C,** larval urodele; **D,** adult urodele; **E,** larval dipnoan; *arc. pal,* palatal arc; *Pt,* pterygoid; *pal,* palatinum; *psp,* parasphenoid; *Pmx,* premaxillary; *Vo,* vomer (**A,B,** after Jarvik, 1954; **C-E,** after Lebedkina, 1979).

that the order in which connections between bones were formed during the larval development of the Rhipidistia (premaxilla to vomer: vomer to parasphenoid) can be traced during phylogeny of that group. Thus in ancient Rhipidistia *(Porolepis, Youngolepis, Powichthys, Thursius, Gyroptychius latvicus)* the vomers are short, widely spaced, have no contact with the parasphenoid and are weakly linked with the premaxilla. That is why they are often missing in fossil material (Vorob'eva, 1977, 1981; Jessen, 1980; Chang Mee-Mann, 1982). The parasphenoid is short and does not reach the internasal region, though exceptions such as *Youngolepis* are known.

In osteolepiform phylogeny it is possible to trace progressive development of the dermal palate. This process can be traced as follows. The vomers become elongate, join, and develop processes (Fig. 4F). Similar changes can be traced in the Anura, particularly in the Pelobatidae as was shown by Roček (1980). Urodeles and anurans, though similar in morphogenesis, have distinctive features. Thus in the Anura the link
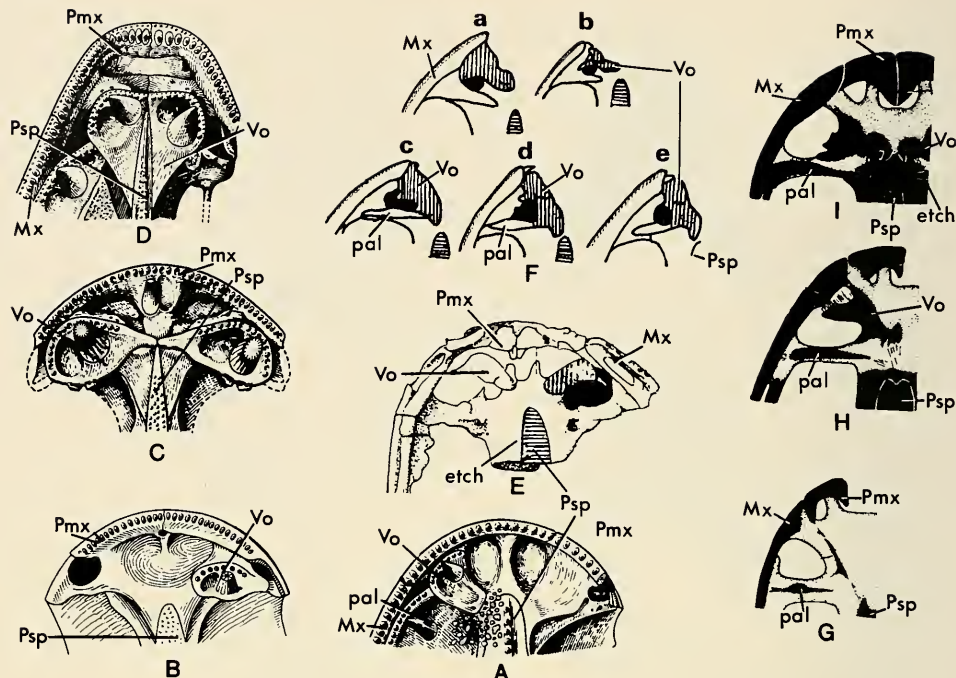
Fig. 4. Comparisons of the palatal surface in Rhipidistia (**A-D**) and Anura (**E-I**). **A,** Porolepiformes (*Porolepis*); **B-D,** Osteolepiformes (**B,** *Thursius;* **C,** *Megalichthys;* **D,** *Eusthenopteron*); **E,** *Eopelobates;* **F,** various primitive anurans (Pelobatidae); **G,** prometamorphic state in *Rana temporaria;* **H,I,** different ontogenetic states (adult) in *Rana esculenta, etch,* ethmosphenoid; *Mx,* maxillary; *Pmx,* premaxillary; *Psp,* parasphenoid; *pal,* palatinum; *Vo,* vomer. (**C-D,** from Jarvik, 1980; **E-F,** from Roček, 1980; **G-I,** from Lebedkina, 1979).

between the premaxilla and vomer develops at the end of metamorphosis and then reduces (Fig. 4**G**), as is known in a clearly-defined way only in *Xenopus* and *Ascaphus* (Lebedkina, 1979). The tendency to reduce the ethmoidal endoskeleton and exoskeleton, typical of adult anurans, is expressed in the weakening of the vomers, the absence of vomer-parasphenoid links and the displacement of the premaxilla by the maxilla. However, the palate in some Anura suggests recapitulation of a rhipidistian pattern. In this respect *Eopelobates leptocolaptus* from the Upper Carboniferous is interesting (Roček, 1980). In this form, well-developed premaxillaries are preserved. They may contact the vomers (Fig. 4), which in this form are of primitive shape, being short, widely spaced, and well separated from the parasphenoid. *Amphibamus grandiceps* from Mazon Creek, noted above, adds to this picture. It probably represents a juvenile dissorophoid form (Bolt, 1979), and displays the primitive gnathostome condition for the palate — an undivided palatal arch covered by a shagreen of teeth.

In the presence of a shagreen of denticles this form resembles the ancient crossopterygian *Youngolepis*. Palatal tooth arrangement in *Amphibamus grandiceps* 'is also similar to that of lissamphibians, which commonly have a row of bicuspid pedicellate palatal teeth in a short row sub-parallel to the marginal tooth row' (Bolt, 1979: 555). It is for this reason that juvenile dissorophids can be regarded as lissamphibian ancestors. According to Bolt (1979) juvenile features of the ancestors appear in the adult stage of the descendants as a result of paedomorphic evolution (Gould, 1977), and lissamphibians can be viewed as paedomorphic dissorophoids.
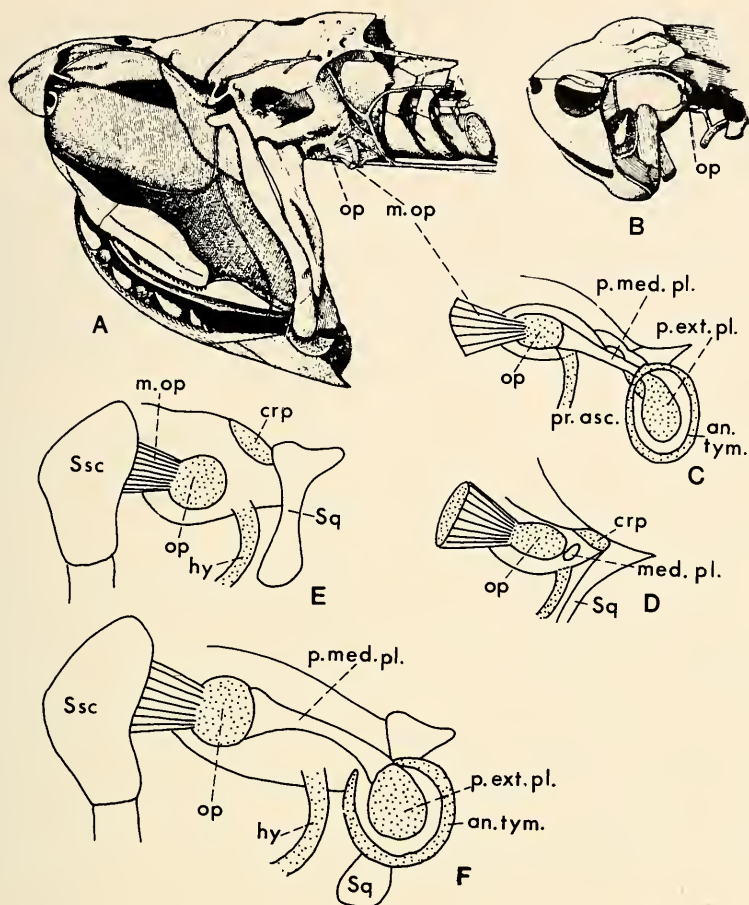
Fig. 5. Structure of the otic region in rhipidistians and anurans. **A,** *Eusthenopteron foordi;* **B,** *Pelobates fuscus;* **C-F,** middle ear structure (**C,** *Rana ricketti;* **D,** reduced state in *Bombina orientalis;* **E,** reduced state in *Microhyla heymonsi;* **F,** *M. berdmorei. an. tym,* annulus tympanicus; *crp,* crista parotica; *hy,* hyoideum; *m. op,* opercular muscle; *op,* opercula; *p.ext.pl,* pars externa plectri; *p.med.pl,* pars media plectri; *Sq,* squamosal; *Ssc,* suprascapula. (**A,B,** from Jarvik, 1975; **C-F,** from Smirnov, 1983).

This example shows that various different comparisons must be made when homologies are looked for between urodeles or anurans and ancient amphibians (labyrinthodonts) or fishes, depending upon the evolutionary stability of the structures concerned. Thus we may compare adult recent forms with their larvae, adult recent with fossil forms, or recent larvae with adult fossil forms (rhipidistians in particular). The principles and advantages of such wide-ranging comparisons were discussed by Roček (1980).

The wide occurrence of heterochrony and parallelism in the fish-tetrapod transition shows that caution must be exercised in reaching any phylogenetic conclusions based on comparison of separate structures or in making direct extrapolations of recent particularities to structures observed in fossil forms. A good example to illustrate this point is the otic region of the skull. The form of the stapes and the condition of otic notch are widely used as phylogenetically significant features of early tetrapods. But the

study of the middle ear in modern amphibians and lizards (by the methods of comparative anatomy, embryology, physiology and morphometry) has demonstrated considerable variability in its morpho-functional condition. Thus the operculum in the foramen ovalis is weakly developed in arboreal amphibians (Hylidae and Rhacophoridae), and a marked reduction in the middle ear may be traced in the transition from terrestrial to aquatic and burrowing amphibians (Fig. 5C-F).

The first stage in this transition appears to be the enlargement of the *pars externa plectri* (Smirnov, 1983). As a result the surface of the tympanic membrane becomes smaller, and its mass and rigidity increase. This leads to a reduction in frequency range acceptability. In the next stage the tympanic membrane is overlain by depressor mandibulae muscle, and the pars externa plectri increases further in size, with a reduction of the ascending process. The annulus tympanicus disappears, and the plectrum degenerates. In extreme cases (*Pelobates, Bombina, Ascaphus,* etc.) all traces of the middle ear (with exception of opercula) may disappear.

Thus, in families at different stages of phylogenetic development (Leiopelmidae, Pelobatidae, Microhylidae), different degrees of middle ear reduction are noted as a result of adaptation to a burrowing way of life *(Microhyla butleri, M. heymonsi, Pelobates fuscus)* or to the torrent-dwelling mode *(Ascaphus truei)*.

It has been shown also that in a number of Anura (Hylidae, Bufonidae Microhylidae, Ranidae) the middle ear is non-functional, and completely reduced in the adult. A definitive condition of middle ear development is observed only in the mature stage. These observations on modern forms show that past evolutionary changes in middle ear structure may have been much more complex than indicated by the application of traditional principles of comparative anatomy to the study of fossils known only from adults. Morphological change at early ontogenetic (larval) stages of development, perhaps involving secondary reduction of previously evolved structures, may have significantly altered the course of evolution in the labyrinthodont middle ear. The possibility of the latter mode was demonstrated on brachiopoid labyrinthodonts (Shishkin, 1975), and the many modifications in the state of the acoustic system in recent Amphibia indicates the possibility of such modifications having occurred in fossil forms as well. As already noted, the morphofunctional analysis applied to the acoustic system of recent forms shows that caution should be exercised in applying structural principles based on recent forms to an interpretation of their possible ancestors.

Thus the otic opercula and opercular muscle have been reconstructed in *Eusthenopteron foordi* by Jarvik (1975). This is a typical representative of the Osteolepiformes which is assumed by Jarvik to be an anuran ancestor (Fig. 5A). However, the opercula was obviously developed as a terrestrial adaptation (Noble, 1931), probably to transmit substratum oscillations from the extremities via the shoulder girdle to the inner ear. However, *Eusthenopteron* is clearly an aquatic form, with no need for such a sound-transmitting mechanism, nor for a tympanic membrane, since the acoustic resistance of body tissues and water are practically the same (Vorob'eva and Smirnov, 1982).

It is possible that sound oscillations of lower frequencies could have been transformed into mechanical oscillations of the fish operculum, and transmitted through the hyomandibula to the inner ear liquid. However, such a mechanism would have been useful only for certain rhipidistians (e.g. *Sauripterus,* Thomson, 1966) which may be assumed to have taken occasional terrestrial excursions, but in such cases there was already a direct way of sound transmission from the limbs and through the shoulder girdle to the occipital region of the skull. The necessity for tetrapod opercula arose only

when the contact between the skull and the shoulder girdle had been lost, and this happened for the first time in amphibians.

The above examples show that the fish-tetrapod transition may have been complex, and interpretations based only on the principles of classical morphology may be inadequate. These should be supplemented by morpho-functional analyses of structures, and a consideration of the ecological aspects of adaptive radiation in recent groups. Only by such a multi-faceted approach can we expect to understand the biological and functional significance of structural change, and at the same time come closer to comprehending the nature of evolutionary mechanisms. By such a complex historical approach, which traces morpho-functional and structural changes in ontogenetic and phylogenetic series of both fossil and recent forms, might we expect to develop an objective view of the phylogeny of various forms.

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